BREEDING RESEARCH ON SOUTH AFRICAN PLANTS:

III. INTRA- AND INTERSPECIFIC COMPATIBILITY IN *IXIA L., SPARAXIS KER., WATSONIA MILL. and ZANTEDESCHIA SPRENG.*

(Met Opsomming in Afrikaans)

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ABSTRACT

In connection with a breeding programme intra- and inter-specific fertility relationships were investigated in Ixia, Sparaxis, Watsonia and Zantedeschia. All genera and species observed are naturally cross-pollinated but capable of spontaneous self-pollination. In Ixia and Watsonia, however, inbreeding led to a decline in vigour. Interspecific and intersubgeneric crosses without a decrease in the fertility of the progeny were obtained relatively easily in all genera. These results are discussed in the light of their importance for plant-breeding as well as the relationships between breeding experiments and taxonomical units.

INTRODUCTION

Intra- and interspecific fertility-relationships were investigated during the initial stages of a breeding programme on Ixia, Sparaxis, Watsonia (all Iridaceae) as well as Zantedeschia (Araceae). This aspect of the breeding programme aimed at the development of new varieties for commercial floriculture was somewhat limited due to the fact that only those pollinations were made which were of some interest from a plant-breeding point of view. Nevertheless, this study includes experiments with and observations on more than forty species. It is, therefore, not only of importance for plant-breeding with respect to the above genera, but may also be of some interest to plant taxonomy.

PROCEDURE

Most of the plant material used was collected in the natural habitat in the South-Western Districts of the Cape, while some seeds and corms were obtained from commercial sources and also from the National Botanic Gardens Kirstenbosch. All experiments were carried out at the Bien Donné Experimental Farm at Groot Drakenstein, Cape.

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The following species were included: *Ixia conica* Salisb., *I. maculata* L., *I. odorata* Ker., *I. polystachya* L., *I. scariosa* Thunb., *I. speciosa* Andr., *I. viridiflora* Lam., *Sparaxis bulbifera* Ker., *S. grandiflora* Ker., *S. tricolor* Ker. *Watsonia ardernei* Sander, *W. beatricis* Mathews, *W. brevifolia* Ker., *W. bulbillifera* Mathews and L. Bolus, *W. galpinii* L. Bolus, *W. humilis* Mill, *W. marginata* Ker, *W. pillansii* L. Bolus, *W. pyramidata* Andr., *W. spectabilis* Schinz. *W. wordsworthiana* Mathews and fifteen other hybrids and unidentified spp., *Zantedeschia aethiopica* Spreng., *Z. albomaculata* Baill., *Z. macrocarpa* Engl. (= *Z. pentlandii* Whyte), *Z. melanoleuca* Hook., *Z. rehmannii* Engl. and one unidentified species with a yellow, blotched spathe and the cv. Helen O'Connor.

All artificial cross-pollinations and self-pollinations were carried out with the necessary precautions pertaining to emasculation and isolation. The latter was implemented either by covering whole plants with pollination cages or by enclosing the inflorescences in glassine bags. The following data were recorded during several seasons: Number of flowers pollinated, number of flowers which set seed, number of seeds harvested, number of seeds germinated, the vigour and the fertility of the progeny. The significance of the difference between two means was examined by means of a t-test.

RESULTS

(1) *Ixia*. A summary of the results is given in Table 1. They show clearly the superiority of cross-pollinations and the inferiority of the self-pollinations with regard to seed set. The seed set in all cross-pollinations is significantly better than that following self-pollination (P = 0·01 and 0·05 resp.). No differences exist between seed set in open pollinated flowers and that in artificially cross-pollinated ones.

TABLE 1

Summary of results of intra- and interspecific pollinations in *Ixia* and *Sparaxis*

Genus and mode of pollination	% flowers which set seed	No. of seeds per flower set	
		Mean	Mean maximum
Ixia			
open	66·9	12·0 ± 9·4	36·8
artif. intrasp. —x	77·8	15·7 ± 11·8	31·9
artif. intersp. —x	33·4	8·2 ± 7·2	23·7
spontaneous self	26·6	2·7 ± 5·7	21·3
artif. self	23·0	3·1 ± 4·0	15·7
Sparaxis			
open	82·7	10·7 ± 3·7	39·0
artif. intrasp. —x	91·6	14·9 ± 6·4	27·6
artif. intersp. —x	90·2	11·1 ± 11·3	31·3
spontaneous self	28·6	14·5 ± 9·3	29·5
artif. self	47·8	10·5 ± 5·2	21·0

Though all spp. investigated show the same tendency with regard to self-compatibility, it may be mentioned that there are indications that spontaneous self-pollination occurs more frequently in *I. polystachya* and *I. viridiflora*. *I. odorata* is apparently completely self-incompatible.

Germination ability was not affected by the mode of pollination nor was the fertility of the F_1 lost after inbreeding. There was, however, a clear inbreeding depression with regard to general vigour.

The crossability of the different spp., (Fig. 1) shows clearly that interspecific hybridization can be procured relatively easily in Ixia and that even crosses are possible between the subgenera Ixia proper and Morphixia.

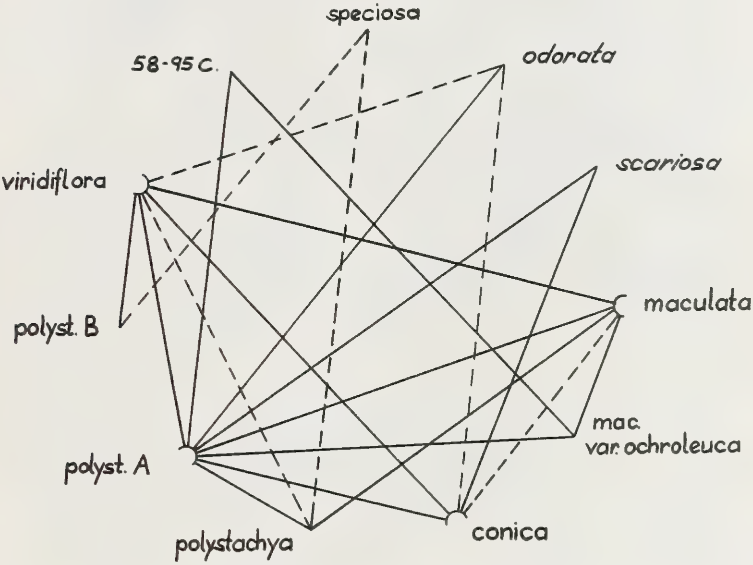

FIG. 1.—Diagram of interspecific crosses made in Ixia.
broken lines—unsuccessful crosses
solid lines—successful crosses
species italicized—Subgenus Morphixia
other species—Subgenus Eu-Ixia

(2) *Sparaxis*. A summary of the results is given in Table 1. As in Ixia the percentage of flowers which set seed after pollination is much lower following self-pollination than that after cross-pollination. But

no differences exist with regard to mean number of seeds per flower set. Similarly, fertility, germination ability and vigour of the F_1 is the same following self- as well as cross-pollination. All three spp. are cross-compatible with each other. There are, however, indications, that the fertility of such species-hybrids is reduced.

(3) *Watsonia.* A summary of the results is presented in Table 2. As can be seen from this, differences exist between the evergreen species and the deciduous species in that the evergreen species are relatively more self-compatible. In both groups the seed set following cross-pollination is superior to that after self-pollination ($P = 0{\cdot}01\%$). Interspecific crosses between the evergreen and the deciduous group were successful, as also crosses between species belonging to the two different subgenera Neuberia and Watsonia. The fertility of the F_1 developed from seeds from self-pollinated flowers was somewhat reduced and the general vigour showed a severe inbreeding effect.

Table 2

Summary of results of intra- and interspecific pollinations in *Watsonia*

Mode of pollination	% flowers which set seed	No. of seeds per flower set	
		Mean	Mean maximum
Deciduous spp.			
open	66·7	15·8 ± 7·7	34·8
artif. intrasp. —x	81·1	6·9 ± 4·9	12·4
artif. intersp. —x	85·3	13·9 ± 6·5	27·9
spontaneous self	7·8	6·1 ± 4·7	16·6
artif. self	16·7	3·9 ± 3·0	8·9
Evergreen spp.			
open	70·6	9·8 ± 2·9	12·5
artif. intrasp. —x	77·3	14·7 ± 5·9	18·8
artif. intersp. —x	89·6	15·7 ± 4·8	23·8
spontaneous self	86·0	7·5 ± 2·4	12·5
artif. self	87·9	9·6 ± 3·5	16·7
decid. x evergr.	46·2	6·1 ± 3·4	16·9

The cross-compatibility of the different spp. is given in Fig. 2. Of 128 artificial interspecific crosses only 21 proved incompatible, 71 of which had either *W. brevifolia* or *W. marginata* (both Subgenus Neuberia) as one parent, the remaining seven were crosses between evergreen and deciduous species. It may be mentioned that most crosses involving *W. brevifolia* succeeded if *W. brevifolia* was used as the pistillate parent. An explanation as to why seed set following intraspecific cross-pollination was low may be sought in the assumption that this kind of pollination was probably an intra-clonal one, that is, for all practical purposes a type of self-pollination.

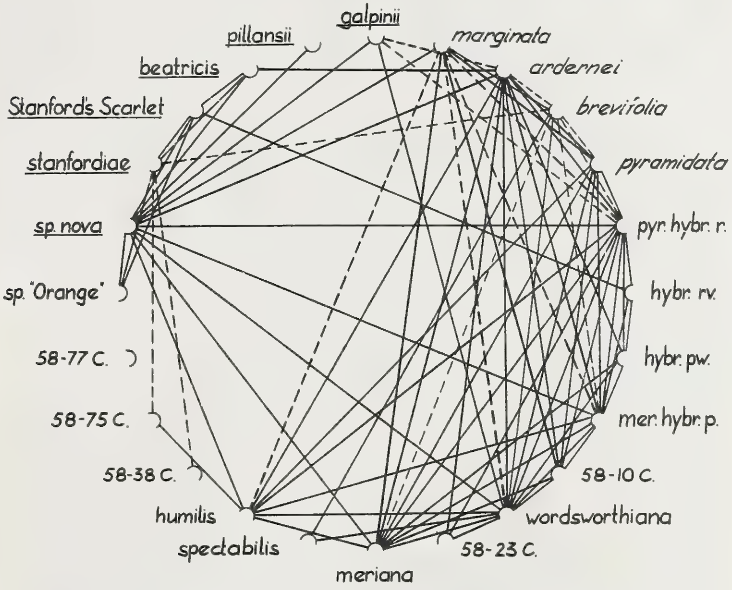

FIG. 2.—Diagram of interspecific crosses made in Watsonia.

broken lines—unsuccessful crosses
solid lines—successful crosses
species italicized—Subgenus Neuberia
other species—Subgenus Eu-Watsonia
species underlined—Evergreen spp.

(4) *Zantedeschia.* The only studies made were those involving the self-compatibility of species and those involving the crossability of species having a coloured spathe with *Z. aethiopica* as the male parent. A summary of the results with regard to seed set is given in Table 3. The percentage of flowers which set seed is an estimate based upon the mean number of flowers per inflorescence as observed over six seasons. With regard to seed set following open-pollination, all spp. tested reacted in the same way and this mode of pollination is superior to seed set following self-pollination and interspecific crosses. ($P = 0 \cdot 01$ and $0 \cdot 05$.) The crossability with *Z. aethiopica* as a pollen parent is highest in

Z. rehmannii and practically nil in an unidentified species with a yellow spathe. The self-compatibility is, with the exception of the same unidentified species, surprisingly high. The vigour of the F_1-progenies is not seriously affected by interspecific crosses or inbreeding. Data pertaining to fertility are not yet available.

TABLE 3

Summary of results of intra- and interspecific pollinations in *Zantedeschia*

Species and mode of pollination	% flowers which set seed	No. of seeds per flower set	
		Mean	Mean maximum
Open, all spp.	80·4	2·5 ± 1·1	4·5
Artif. intersp. —x			
rehmanii	26·4	1·5 ± 0·4	2·7
melanoleuca macrocarpa	8·4		
"yellow"	2·4		
Spontaneous self			
macrocarpa	74·0	1·9 ± 0·7	3·3
melanoleuca	33·0		
rehmanii	40·2		
"yellow"	0		
cv. H. O'Connor	74·7		
Artif. self			
melanoleuca	82·6	1·9 ± 0·9	3·9
rehmanii	66·7		
cv. H. O'Connor	70·0		

It may be mentioned that the success of artificial interspecific pollinations varied considerably from year to year; it is not possible so far to offer an explanation for this.

DISCUSSION AND CONCLUSIONS

Intra- and interspecific fertility-relationships are of the utmost importance for breeding work on any subject, since the choice of a breeding technique and, therefore, the time required for a breeding programme, depend greatly on the breeding system, i.e. the mode of pollination, in the plant concerned.

Experimental evidence was brought forward that—

(1) Cross-pollination is the natural mode of pollination in the genera investigated,

(2) Spontaneous self-pollination is possible in all these genera,

(3) That interspecific crosses within the genera, even between different subgenera are not difficult to obtain,

(4) That inbreeding by selfing leads to a severe decline in vigour in Ixia and Watsonia, while Sparaxis and Zantedeschia suffer no ill effects. From these findings it can be concluded that in Ixia and Watsonia breeding techniques have to be applied as for cross-pollinated plants, capable of vegetative propagation, while in Sparaxis and Zantedeschia techniques can be also employed which are usually limited to self-pollinating plants and which lead to homozygosity in relatively short periods of time.

Crosses of *Z. aethiopica*, a winter-flowering species, with summer-flowering species possessing a coloured spathe have not been reported previously. The attempts to develop vigorous, multi-flowered varieties with coloured spathes is an old problem in horticulture. Thus far it has been tackled by crossing summer-flowering species with each other (Shibuya, 1956; Bailey, 1944). The products of such crosses, however, seem still to lack the flower production potential which makes the commercial production of *Z. aethiopica* so economical. A good opportunity for the development of new varieties which combine the qualities of summer- and winter-flowering species may exist in the production of hybrids between these two groups.

The self-compatibility of Zantedeschia as well as the lack of an inbreeding depression in inbred progenies as found in this study, was also observed by Shibuya (1956).

Crosses between *Watsonia* species of low height such as *W. brevifolia*, *W. humilis* and *W. spectabilis* with large-flowered species as *W. pyramidata* and *W. ardernei* and hybrids belonging to these species are considered of importance for the production of horticultural varieties of a suitable peduncle-length and a type of inflorescence which can be packed and transported easily. Several of the other interspecific crosses may serve in the production of a greater range of flower colours and types.

The success of interspecific crosses in *Ixia* may lead to a combination of a floriculturally superior raceme, as in *I. viridiflora*, with a range of flower colours obtainable in other species. In Sparaxis, long-stemmed forms of *S. bulbifera* may be useful in the production of suitable cut-flower varieties.

The results of this study may contribute further in answering the question to what extent cytogenetical investigation in general and breeding experiments in particular are able to aid plant taxonomy. The species-concept and the other taxonomical units are mainly built on morphological differences by which forms can be classified. Clausen, Keck and Hiesey (1939) proposed a new concept of taxonomical units based on breeding experiments in which crossability and fertility of the progeny play a prominent role. Furthermore, there is one school of geneticists who have attempted to erect reproductive isolation as the only or the most important criterion of a species. Gates (1951) reviewed and clarified the situation regarding this relationship between taxonomic units and cytogenetics. He quoted many genera or large subgenera of plants in which the species are nearly all infertile, and stated that mere divergence does not necessarily produce intersterility and that intersterility can arise in the absence of phenotypic differences.

The breeding experiments in Ixia, Sparaxis and Watsonia support this point of view. In these genera such morphologically different species as *Ixia scariosa* and *I. polystachya*, or *W. brevifolia* and *W. pyramidata* intercross easily and their progeny is fertile. Recently, in Viola a similar situation was reported (Horn, 1956). It would be absurd to lump all the inter-fertile forms into one morphologically divergent mammoth-species. On the other hand, intersterility can well stress existing morphological differences and so lead to the formation of a new species as was the case in another South African genus, namely Bulbinella Kunth (Horn, 1962), where the phenotypically different *B.* var. *latifolia* was put into one species with *B. robusta*, before breeding experiments had been carried out. Breeding experiments can, therefore, be of supplementary help in the circumscription of species as soon as morphological divergence is accompanied by reproductive isolation.

OPSOMMING

In verband met 'n teeltprogram is intra- en interspecies vrugbaarheidsverhoudings by Ixia, Sparaxis, Watsonia and Zantedeschia ondersoek. Al hierdie geslagte is natuurlik kruisbestuiwend, maar spontane selfbestuiwing is ook moontlik. Inteelt lei egter by Ixia en Watsonia tot 'n depressie van groeikrag. Geen groot moeilikheid is ondervind as interspecies en ook inter-subgenus-kruisings uitgevoer is, en die nageslag van sulke kruisings is vrugbaar. Die resultate van hierdie studie is bespreek met betrekking tot planteteelt en die verband wat tussen taksonomiese eenhede en bestuiwings-eksperimente bestaan.

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